



Isotopic niche overlap and partition among three Antarctic seals from the Western Antarctic Peninsula

Silvina Botta^{a,*}, Eduardo R. Secchi^a, Tracey L. Rogers^b, Jonatas H.F. Prado^a, Renan C. de Lima^{a,c}, Pedro Carlini^d, Javier Negrete^e

^a Laboratório de Ecologia e Conservação da Megafauna Marinha, Instituto de Oceanografia, Universidade Federal do Rio Grande-FURG, Rio Grande, RS 96203900, Brazil

^b Evolution & Ecology Research Centre, School of BEES, University of New South Wales, Randwick, NSW 2052, Australia

^c Programa de Pós Graduação em Oceanografia Biológica, Instituto de Oceanografia, Universidade Federal do Rio Grande-FURG, Rio Grande, RS 96203-900, Brazil

^d Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata (CP1900), Buenos Aires, Argentina

^e Departamento de Biología de Predadores Tope, Instituto Antártico Argentino, Av. 25 de Mayo 1143, San Martín, Buenos Aires C101 AAZ, Argentina

ARTICLE INFO

Keywords:

Ecological niche
Western Antarctic Peninsula
Pack ice seals
Stable isotopes

ABSTRACT

In the present study we used stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) analysis of whiskers to investigate the isotopic niche overlap and partition among three pack ice seals sampled along the Danco Coast, Western Antarctic Peninsula (WAP). Isotopic values in serially sampled whiskers of 34 leopard (*Hydrurga leptonyx*, HL), 13 crabeater (*Lobodon carcinophaga*, LC) and 14 Weddell (*Leptonychotes weddellii*, LW) seals were measured. Two clusters of leopard seals were identified based on their $\delta^{15}\text{N}$ values: a high-trophic level group (HL_{high}) and a low-trophic level group (HL_{low}). Overlap in SEAc was only seen between HL and LC, while HL and LW showed an overlap in their convex hulls, but no overlap in SEAc. Diet compositions estimated using Bayesian stable isotope mixing models revealed intra- and interspecific differences among seals. For leopard seals highest dietary contributor was krill, while for HL_{high} krill and fish_cephalopod were the main contributors. Mixing models run separately for each HL seal showed a large variation in the proportional contribution of krill (12–90%) compared to the other sources (cephalopods, fish, penguins and seals). The crabeater seals almost exclusively consumed krill, with a low contribution of the other prey. Weddell seals, on the other hand, showed a high proportion of fish and a lower contribution of cephalopods and penguins, while the contribution of krill seemed to be minimal. This study is the first to compare isotopic niches of three Antarctic seals from the WAP. Our results indicate that crabeater and leopard seals seem to have a strong and a considerable dependence on krill, respectively. Although the WAP is characterized by an unusually high production of Antarctic krill the large community of vertebrate predators that feed upon this resource (penguins, seals and baleen whales) should be especially vulnerable under future scenarios of reduction of krill biomass. Under the current drastic environmental changes in the WAP, continuing to monitor WAP seal diets and the relative contribution of krill to them will help understand the degree to which climate change may alter the population dynamics of these upper trophic level species.

1. Introduction

The marine ecosystem of the western Antarctic Peninsula (WAP) is a highly productive marine environment that is experiencing strong sea ice decreases and warming during the last few decades (Ducklow et al., 2013). It has been well documented that these changes, summed to pollution, past exploitation of marine mammal species (i.e. whales and seals), and current exploitation of fish and krill stocks have a variety of negative effects on the ecosystem (Forcada et al., 2012). Changes in penguin species composition, for example, have been documented in the Palmer region, where ice-obligated Adélie penguin (*Pygoscelis*

adeliae) colonies are being replaced by non-ice requiring Gentoo penguins (*P. papua*) (Trivelpiece et al., 2011; Lynch et al., 2012). However, sea-ice retreat seems not to be the only driver of population changes, but the indirect effect of this condition through its impact on the abundance of krill might be affecting more the krill-dependent Adélie penguins than Gentoo penguins which have a broader trophic diversity (Trivelpiece et al., 2011).

Krill also support a large population of crabeater seals (*Lobodon carcinophaga*) and Antarctic fur seals (*Arctocephalus gazella*) in the WAP, along with leopard seals (*Hydrurga leptonyx*) and whales (Forcada et al., 2012; Southwell et al., 2012; Seyboth et al., in this issue). The

* Corresponding author.

E-mail address: silbotta@gmail.com (S. Botta).

contrasting pattern of high densities of krill close inshore, instead of the typical more offshore distribution of this resource, in the Antarctic Peninsula (Atkinson et al., 2008) might play a role in the large number of krill consumers in this region. Although leopard seals are typically considered top predators (Rogers, 2009), a large part of the diet of WAP leopard seals includes krill (Rogers et al., 2016). Their dental and mouth anatomies allow this predator to consume large and small prey, thus occupying both upper and lower trophic positions within the food webs (Zhao et al., 2004; Rogers et al., 2016). Although a seasonal switch between high-trophic level prey in austral summer and low-trophic level prey in austral winter was reported (Lowry et al., 1988; Hall-Aspland et al., 2005a; Rogers et al., 2016), their preference for krill in areas where this resource is abundant, as the WAP (Atkinson et al., 2008), seems to occur also during summer months (Casaux et al., 2009, 2011). In other regions, the species feeds mostly on higher-trophic level prey, such as fish, penguins and seals (Hall-Aspland and Rogers, 2004; Hall-Aspland et al., 2005a; Zhao et al., 2004). Crabeater seals are highly specialized invertebrate consumers, with finely divided lobed teeth that allow the efficient capture of krill (Bengtson, 2009). In the WAP, the species also depend almost exclusively on this resource (Lowry et al., 1988; Hückstädt et al., 2012; Guerrero and Rogers, 2017) although some fish and squid are included in order to supplement their diet. Weddell seals (*Leptonychotes weddellii*), on the other hand, are mainly piscivorous with a minimal contribution of krill to their diet (Dearborn, 1965; Casaux et al., 2006, 2011; Southwell et al., 2012).

In this context, current bottom-up effects of krill stocks depletion may also threaten krill-dependent seal populations by influencing foraging behavior, reproductive success and survival of these predators (Forcada et al., 2012; Seyboth et al., 2016). In turn, shifts in abundances of these apex components of Antarctic oceans may drive future top-down effects, accentuating ecosystem changes in the WAP. Therefore, the improved knowledge and long-term monitoring of diet composition and trophic niche overlap among these important components of the WAP food web will allow a better understanding of their role in structuring this threatened ecosystem and on the potential effect of changes to their own survival.

Stable isotopes analysis (SIA) has been used extensively to examine the diet of marine mammals (Schell et al., 1989; Zhao et al., 2004; Witteveen and Wynne, 2016). Stable isotopic composition of a consumer reflects the mixture of their assimilated prey (Peterson and Fry, 1987). However, a predictable enrichment in ^{15}N over ^{14}N and in ^{13}C over ^{12}C in predators relative to their prey occurs. This enrichment, called Trophic Discrimination Factor (TDF), is large (3–5‰) in the case of $\delta^{15}\text{N}$ values and small (0–1‰) in $\delta^{13}\text{C}$ values; hence, they are useful indicators of trophic position and habitat occupancy, respectively (Deniro and Epstein, 1978; Hobson et al., 1996; Martínez Del Río et al., 2009; Newsome et al., 2010). By providing information on the diet and the habitat, some dimensions of the ecological niche (Hutchinson's n -dimensional hypervolume, Hutchinson, 1957) can be assessed by SIA. Indeed, the isotopic niche can be delineated in a bi-plot representing its bionomic ($\delta^{15}\text{N}$) and scenopoetic ($\delta^{13}\text{C}$) axes (Bearhop et al., 2004; Newsome et al., 2007). Furthermore, advances in isotopic modelling allow the estimation of the most probable proportion of prey that contribute to the mixing observed in the consumer's tissues (Parnell et al., 2010). Consequently, by describing the isotopic niche and the proportional composition of the diet of a predator, SIA provides a more comprehensive understanding on the trophic ecology of a species.

Moreover, the isotopic composition of different tissues integrates the diet over the period they were synthesised (Tieszen et al., 1983; Dalerum and Angerbjörn, 2005). Thus, tissues will provide information on the feeding ecology of different time frames depending on their turnover rates (Martínez Del Río et al., 2009). In the case of phocid whiskers the diet can be recorded over months and up to one year (Hall-Aspland et al., 2005a, 2005b; Rogers et al., 2016). Furthermore, the sampling of this tissue has the advantage of being minimally invasive (Newsome et al., 2010; Beltran et al., 2015; Rogers et al., 2016), thus

allowing the examination of a large number of specimens.

This is the first study to estimate and compare the diet of three seal species inhabiting the WAP by using a stable isotopic approach. The outcomes of this study include (1) the determination of the influence of species, sex and year of capture on the stable isotope composition of whiskers of leopard, Weddell and crabeater seals from WAP; (2) the estimation of the isotopic niche overlap among the three species, and (3) the quantification of the contribution of main putative prey items to the seals diet.

2. Methods

2.1. Seal capture and study area

Field work was conducted along the Danco Coast, Western Antarctic Peninsula (Argentine Antarctic Station “Primavera”, 64°09' S 60°57' W), in late January/February of 2011, 2014 and 2016. A total of 13 crabeater (LC), 14 Weddell (LW) and 34 leopard seals (HL) were immobilised using a teleinject air gun darting system when hauled out on ice floes. All seals were darted from a boat or from the ice and sedation was achieved using a combination of tiletamine/zolazepam 250 mg (Higgins et al., 2002). Following immobilization, standard length (nose to tail) and body mass (van den Hoff et al., 2005) were recorded and a whisker was plucked from each individual. Based on the measurements, all sampled seals were classified as adults in the case of HL and as juveniles or adults in the case of LC and LW. Sex was determined by visual inspection of the external genitalia.

2.2. Stable isotope analysis

All whiskers were washed with an ethanol-methanol 1:1 mixture for lipids removal, allowed to air dry and sub-sampled every 5 mm using nail clippers. In some cases, sections were > 5 mm in order to achieve a mass of 0.7 mg, mainly close-to-tip sections. Samples were placed in tin capsules and analyzed using a Costech (4010) elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (UNM-CSI). Isotope data are expressed in delta (δ) notation which for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where R_{sample} or R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios in the sample or standard for carbon and nitrogen. Internationally accepted standards are Vienna Pee Dee Belemnite (V-PDB) limestone and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The weight percent carbon to nitrogen concentrations ratios of all vibrissae samples was also determined and ranged between 2.8 and 3.3 (Table S1). These values were within the range of theoretical ratios for keratin (Newsome et al., 2009). Delta values were calculated using multiple-point normalization. The internal laboratory standards used were soy protein, whey protein, casein, tuna, IAEA-N1, IAEA-N2, USGS-4 and USGS-43. Analytical precision (SD) of these internal standards was measured to be < 0.2‰ for $\delta^{15}\text{N}$ and < 0.04‰ in the case of $\delta^{13}\text{C}$.

2.3. Data analysis

Linear plots of whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values against the distance from the tip (oldest formed) of the whisker were produced for each individual seal.

In the case of leopard seals, a large variation in $\delta^{15}\text{N}$ values was found (see Section 3) and at least two potential groups of consumers were identified in the individual line plots, where some individuals seem to prey upon low-trophic level prey (e.g. krill) and some others occupy higher trophic positions (i.e., show higher mean $\delta^{15}\text{N}$ values) (Fig. 1). Therefore, a cluster analysis was conducted to identify the groups within the isotope data and to allow for the assignment of individuals to a low or to a high-trophic level group. The function *pam* from the *cluster* package in R (Maechler et al., 2017) was used. The

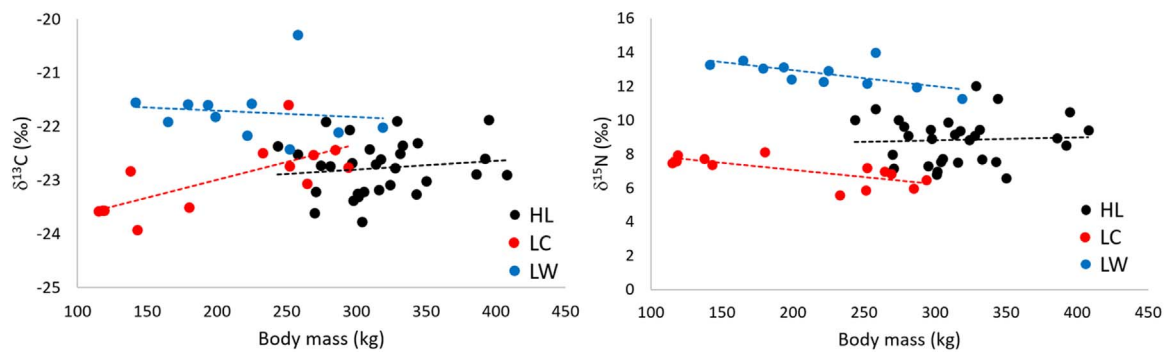


Fig. 1. Relationship between body mass and mean whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for leopard (HL), crabeater (LC) and Weddell (LW) seals from the Danco coast, Western Antarctic Peninsula. The linear regression lines area shown for each species (dashed lines).

method provides a measure of cluster validity that determines the optimum number of clusters in a dataset by using average silhouette widths. If the average silhouette width is close to one, the fit can be considered as good. In general, values of average silhouette width > 0.70 are considered as to represent a strong structure within the data and values between 0.51 and 0.70 show a reasonable structure to the clusters (Kaufman and Rousseeuw, 1990).

Linear mixed models (LMM) (Pinheiro and Bates, 2000) were used to examine the effects of species, sex (both as fixed effects) and their interactions on whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The models used individual identity as the random effect to account for repeated measures of each response variable on the different whisker segments. The two distinct groups of leopard seals identified in the cluster analysis (see Section 3), were considered as two different “species” in the model. Sampling year was not included as a covariate because HL individuals were sampled in different years than LC and LW, thus, this factor was tested in species individual models (see below).

We started with the full model and examined interaction first and then, the random effect term was added to the model. After that, the variables that did not improve the fit of the model ($p > 0.05$) were excluded. Model selection was based on Akaike's Information Criterion (AIC) and the likelihood ratio test (see Zuur et al. (2009) for more details about model selection). The goodness-of-fit of each model was estimated from marginal ($R^2 \text{ LMM}_{(m)}$) and conditional ($R^2 \text{ LMM}_{(c)}$) coefficients of determination, following Nakagawa and Schielzeth (2013). The former shows the proportion of the variance explained by the fixed effects only, while the second shows the proportion of the variance explained including the random effects. The final models were validated using diagnostic plots.

To test the sampling year effect on the whisker segments $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on individual species, LMMs were fitted using the *nlme* (Pinheiro et al., 2017) and *piecewiseSEM* (Lefcheck, 2016) packages. All analyses and visualizations were performed in the R statistical environment (R Development Core Team, 2013) and a significance level of 0.05 was adopted.

In order to test for the relationship of body mass on seals' mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values linear regression tests were performed. We decided to test for the effect of this variable on isotopic values separately (i.e. not including them as explanatory values in LMMs) for two reasons: first, because LW seals sampled in 2014 did not have their body mass measured; second because we would have to use whisker mean isotopic values instead of individual segment values, reducing the explanatory power of the model.

In order to assign time-scales to isotopic data along whiskers, species-specific growth models are needed (Rogers et al., 2016). Models were developed for Phocidae species such as northern elephant seals (*Mirounga angustirostris*, Beltran et al., 2015) and leopard seals (Rogers et al., 2016). These studies reported whisker growth trajectories as non-linear and with parameters varying among whiskers from different positions across the mystacial cheek (Beltran et al., 2015; McHuron

et al., 2016; Rogers et al., 2016). No information on the insertion position of the plucked whiskers used in the present work was available. Furthermore, due to the high variability found among growth trajectories and molting patterns in phocids, it is not recommended to extrapolate growth dynamics developed for one species to another (Beltran et al., 2015; McHuron et al., 2016; Rogers et al., 2016). Therefore, due to the lack of information about the whisker follicle position and that species-specific growth models for Weddell and crabeater seals are not available, no specific time frames were assigned to each subsample along the whisker. However, it was assumed that the sum of subsamples integrates the diet of the individual during an unknown number of months up to a year preceding the sampling date (end of January/February – austral summer) (Hirons et al., 2001; Rogers et al., 2016).

2.3.1. Isotopic niche width and overlap

Bayesian Layman's isotope metrics $\delta^{15}\text{N}$ range (NR) and $\delta^{13}\text{C}$ range (CR) (Layman et al., 2007) were estimated for each species using Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011) in order to investigate the trophic diversity and niche diversification at the base of the food web.

The isotopic niches of each species were estimated using calculated convex hull areas and by generating bivariate ellipses in SIBER (Jackson et al., 2011). Standard ellipses corrected for small sample size (SEAc) were estimated as a measure of the mean core group isotopic niche for each group of seals. The overlap area between paired SEAc and convex hulls were calculated and the respective percentage of overlap area was estimated for each group. Additionally, the Bayesian standard ellipse areas (SEA_B) were also calculated in order to obtain unbiased estimates of the isotopic niche widths with credibility intervals (Jackson et al., 2011). This procedure was repeated by calculating the isotopic niche areas and overlap between the two groups of HL seals (HLhigh and HLlow – HL with relative high end low trophic levels), LC and LW.

2.3.2. Stable isotope mixing models

The relative contribution of potential prey to the diet of the seals was estimated using the Bayesian mixing model in the package *simmr* (Parnell, 2016) developed for the R statistical environment (R Development Core team, 2013). Based on previous studies that described the crabeater, Weddell and leopard seals' diet in the Antarctic Peninsula (Lowry et al., 1988; Casaux et al., 2006, 2011; Daneri et al., 2012; Negri et al., 2016; Rogers et al., 2016) we selected published isotopic data for their main prey items from the WAP. Prey items were lumped into five distinct groups: krill, fish, cephalopods, penguins and seals (Table 1). Models for HL included krill, fish, cephalopods, penguins and seals as sources (Casaux et al., 2011; Rogers et al., 2016). In the case of LC, fish and krill were used as sources (Hückstädt et al., 2012). The contribution of krill, fish, cephalopods and penguins were included in mixing models for LW (Casaux et al., 2006, 2011; Acevedo

Table 1

Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each prey species and the five groups (in bold) used in the Bayesian mixing models to estimate diet composition of seals.

Prey	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Source
Krill			
<i>Euphasia superba</i> (mean)	-27.1 ± 0.8	3.5 ± 0.5	Kokubun et al. (2015), Dunton (2001), Polito and Goebel (2010), Polito et al. (2013)
Fish			
<i>Chionodraco rastrospinosus</i>	-25.9 ± 0.1	7.6 ± 0.2	Mincks et al. (2008)
<i>Gobionotothen gibberifrons</i>	-24.9 ± 0.3	10.7 ± 0.3	Mincks et al. (2008)
<i>Pleuragramma antarcticum</i>	-24.7 ± 0.4	9.4 ± 0.5	Polito et al. (2011)
All fish (mean)	-25.2 ± 0.3	9.2 ± 0.3	
Cephalopods			
<i>Pareledone</i> sp.	-24.5 ± 0.1	9.1 ± 0.3	Mincks et al. (2008)
Penguins			
<i>Pygoscelis adeliae</i>	-23.7 ± 0.3	10.2 ± 0.4	Dunton (2001), Polito et al. (2011)
<i>P. papua</i>	-23.3 ± 0.6	8.9 ± 0.7	Polito et al. (2011)
All penguins (mean)	-23.6 ± 0.4	9.9 ± 0.5	
Seals			
<i>Arctocephalus gazella</i>	-24.3 ± 1.1	10.2 ± 0.9	Polito and Goebel (2010)

et al., 2015; Bombosch and Solovyev, 2017).

Mean isotopic values of vibrissae were used for population-level analyses of dietary proportion of HL, LC and LW seals. Additionally, due to the large variation observed in $\delta^{15}\text{N}$ values of HL (see Results) individual-level mixing models using all segment values were run for this species. Three sets of trophic discrimination factors (TDFs) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were tested. The adequacy of prey database and these discrimination factors was checked using a simulated mixing polygons following Smith et al. (2013), using the packages *sp* and *splanx* in R, before running the mixing models. The first set of TDFs was calculated as the mean (\pm SD) value of the TDF values for whiskers derived from captive feeding trials of seals from six Phocidae species ($\Delta^{13}\text{C}$ LC and $\Delta^{15}\text{N}$ for the first eight values of whisker TDFs, Table 4 in Beltran et al. (2016)). Based on that study, TDFs of $3.4 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$ and $3.2 \pm 0.5\text{‰}$ for $\delta^{15}\text{N}$ were the first set tested in the mixing polygons. The other two sets of TDF values were those reported by Hobson et al. (1996) (3.2 ± 0.2 and $2.8 \pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) and by Newsome et al. (2010) (2.2 ± 0.7 and $3.5 \pm 0.6\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). The latter were calculated for the sea otter (*Enhydra lutris*) and were used in Bayesian isotopic mixing models for crabeater seals reported in Hückstädt et al. (2012).

3. Results

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured in 689 samples obtained from the 61 seals from the Danco Coast. The mean number of samples per individual was 11 (\pm 5.1), however it varied among seal species as the mean vibrissae length differed among them (Weddell > crabeater > leopard). The mean C:N values of all samples was 3.0 (\pm 0.1) (Table S1).

Overall, mean vibrissa $\delta^{13}\text{C}$ values ranged from -23.8 to -21.9‰ ($-22.8 \pm 0.5\text{‰}$), -23.9 to -21.6‰ ($-23.0 \pm 0.6\text{‰}$) and -22.4 to -20.1‰ ($-21.6 \pm 0.6\text{‰}$) for leopard, crabeater and Weddell seals, respectively. Mean $\delta^{15}\text{N}$ values spanned from 6.6 to 12.0‰ ($8.9 \pm 1.3\text{‰}$) for leopard seals, from 5.6 to 8.1‰ ($7.0 \pm 0.8\text{‰}$) in the case of the crabeater seals and from 11.3 to 14.0‰ ($12.7 \pm 0.7\text{‰}$) for Weddell seals.

Individual isotopic variations along the length of whiskers from HL seals showed low variability in $\delta^{13}\text{C}$ values (Fig. S1). In the case of LC

some fluctuations in carbon isotope values were identified in adults (e.g. LC1, LC6, LC9) while almost no variability was found along the juvenile whiskers (e.g. LC5, LC8, LC 3) (Fig. S3). Weddell seals showed some oscillations and peaks in $\delta^{13}\text{C}$ values, with two animals exhibiting peaks of low ^{13}C -enriched $\delta^{13}\text{C}$ values (Fig. S5). High variability in $\delta^{15}\text{N}$ values was found among leopard seals where some individuals showed consistently high (e.g. HL14, HL22, HL31) or low (e.g. HL2, HL3, HL10) $\delta^{15}\text{N}$ values along the whisker. Furthermore, the $\delta^{15}\text{N}$ profile of some individuals fluctuated between high and low values along the whisker (Fig. S2). In the case of crabeater seals, nitrogen isotopic profiles showed low variability in the values of adult individuals (e.g. LC1, LC6, LC9, LC10) while juveniles had a peak of ^{13}N -enriched $\delta^{15}\text{N}$ values along the whisker (e.g. 3, LC5, LC12) (Fig. S4). Weddell seals showed consistently high $\delta^{15}\text{N}$ values along the whisker with no substantial variability in general (Fig. S6).

Two clusters of leopard seals provided the highest average silhouette width (0.65) using $\delta^{15}\text{N}$ values; indicating a reasonable structure to clusters (Kaufman and Rousseeuw, 1990). The low-trophic level cluster (HL_{low}) was composed of 12 individuals (mean $\delta^{15}\text{N}$ = 7.4‰) and 22 leopard seals were included in the higher-trophic level cluster (HL_{high}, mean $\delta^{15}\text{N}$ = 9.7‰). Therefore, these two clusters were considered as separate groups in both the LMM and the some of the isotopic niche modelling.

The proportion of the variance explained increased when the random effect was included, indicating that this term improves the explanatory power of the model for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. LMM 4 was considered the best model for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, as the inclusion of sex and the interaction term between sex and species did not improve the model fit. Mean $\delta^{15}\text{N}$ values significantly differed between species, with LW having higher and LC lower values than HL. For $\delta^{13}\text{C}$, the mean values followed the same pattern (Table 2). The sampling year effect was not statistically significant for the three species (Table 3).

$\delta^{15}\text{N}$ values were not significantly correlated with body mass in the case of HL (p = 0.76). However, $\delta^{15}\text{N}$ values showed a significant negative correlation with body mass in the case of LC (R^2 = 0.52, p < 0.05) and LW (R^2 = 0.42, p = 0.03). In the case of $\delta^{13}\text{C}$, only LC showed a significant positive correlation with body mass (R^2 = 0.52, p < 0.05) (Fig. 1).

3.1. Isotopic niche width and overlap

Bayesian Layman's NR and CR values were higher in leopard seals than in crabeater or Weddell seals. Isotopic niche areas, represented by convex hulls and both SEAc and SEAB, were larger in LC than in the other two species. Low-trophic level leopard seals showed a smaller SEAc and convex hull than high-trophic level conspecifics (Table 4). Overlap in SEAc was only seen between HL and LC, while HL and LW showed an overlap in their convex hulls, but no overlap in SEAc. HL_{high} and HL_{low} groups of leopard seals did not have an overlap in their SEAc, but showed some overlap between their convex hulls. An almost complete overlap in SEAc and convex hulls was observed between HL_{low} and crabeater seals. Some overlap among convex hulls was also present between HL_{high} and LC and LW (Table 5, Fig. 2).

3.2. Diet composition

The mixing polygon simulation revealed that 2 of the 34 HL individuals and 2 of the 13 LW seals occur outside of all possible mixing polygons using the TDFs obtained from the values reported in Beltran et al. (2016) (Fig. S7). Mixing polygons models using the other two sets of TDF values (Newsome et al., 2010; Hobson et al., 1996) showed equal or more individuals falling outside the outermost contour. In the case of the crabeater seal, all TDF sets showed a considerable percentage of consumers outside the outermost contour 35–100%, with the better performance observed while using Hobson et al.'s TDFs and Beltran et al.'s where 5 and 6 out of 14 consumers falling outside the

Table 2

Summary of statistical output from the linear mixed models* applied to analyze the influence of sex and species on whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of two groups of leopard (low-trophic level, HL_{low} and high-trophic level, HL_{high}), crabeater (LC) and Weddell (LW) seals from the Danco coast, Western Antarctic Peninsula. Estimates and statistical significance (in parentheses) of the fixed factors (sex and species and their interactions) are shown for each variable. The AIC (Akaike's information criterion), the ANOVA, R^2 , and the marginal ($R^2_{\text{LMM(m)}}$) and conditional ($R^2_{\text{LMM(c)}}$) coefficients of determination are shown in the last columns. Lower AIC are shown in bold.

Linear mixed models for whisker $\delta^{15}\text{N}$ values

Model	Intercept	Species (HL_{low})	Species (LW)	Species (LC)	Sex (males)	Species*sex (HL_{low})	Species*sex (LW)	Species*sex (LC)	AIC	ANOVA	R^2	$R^2_{\text{LMM(m)}}$	$R^2_{\text{LMM(c)}}$
1	9.70(0.00)	-2.72(0.00)	-2.61(0.00)	2.46(0.00)	-0.10(0.47)	0.57(0.09)	0.28(0.27)	0.94(0.00)	2019.4	-	0.80	-	-
2	9.67(0.00)	-2.56(0.00)	-2.65(0.00)	2.59(0.00)	0.04(0.88)	0.27(0.68)	0.27(0.61)	0.60(0.23)	1863.0	0.00	-	0.79	0.87
3	9.55(0.00)	-2.41(0.00)	-2.51(0.00)	2.91(0.00)	0.29(0.15)	-	-	-	1860.3	0.63	-	0.79	0.87
4	9.69(0.00)	-2.31(0.00)	-2.56(0.00)	2.92(0.00)	-	-	-	-	1859.0	0.13	-	0.79	0.87
Linear mixed models for whisker $\delta^{13}\text{C}$ values													
1	-22.51(0.00)	-0.26(0.22)	-0.53(0.00)	0.90(0.00)	-0.16(0.11)	Species*sex (HL_{low}) -0.20(0.40)	Species*sex (LW) 0.23(0.21)	Species*sex (LC) 0.14(0.32)	AIC	ANOVA	R^2	$R^2_{\text{LMM(m)}}$	$R^2_{\text{LMM(c)}}$
2	-22.52(0.00)	-0.18(0.68)	-0.45(0.08)	0.99(0.00)	-0.11(0.63)	-0.35(0.48)	-0.001(0.99)	-0.03(0.92)	1549.5	-	0.38	-	-
3	-22.49(0.00)	-0.45(0.02)	-0.46(0.02)	0.97(0.00)	-0.16(0.2)	-	-	-	1306.9	0.00	-	0.38	0.66
4	-22.57(0.00)	-0.51(0.01)	-0.43(0.03)	0.97(0.00)	-	-	-	-	1301.6	0.89	-	0.38	0.65
									1298.8	0.24	-	0.38	0.65

*Model:

Model 1: species + sex + sex*species.

Model 2: species + sex + sex*species + random effect.

Model 3: species + sex + random effect.

Model 4: species + random effect.

Table 3

Estimates and statistical significance (in parentheses) of the effect of sampling year on whisker $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of leopard (HL), crabeater (LC) and Weddell (LW) seals from the Danco coast, Western Antarctic Peninsula. The random term was included into the analyses.

Isotope	Species	Intercept	year(2014)	year (2016)
$\delta^{15}\text{N}$	LC	7.19(0.00)	-	-0.08(0.87)
	LW	12.44(0.00)	-	0.21(0.66)
	HL	8.72(0.00)	0.33(0.47)	-
$\delta^{13}\text{C}$	LC	-22.62(0.00)	-	-0.46(0.31)
	LW	-21.12(0.00)	-	-0.62(0.16)
	HL	-22.66(0.00)	-0.18(0.24)	-

Table 4

Convex hulls (CH), standard ellipse areas for small sample sizes (SEAc) and Bayesian standard ellipse areas (SEA_B) and their respective 95% credibility intervals (CI) of leopard seals (population level, HL, and the two groups, low-trophic level, HL_{low} and high-trophic level, HL_{high}), crabeater seals (LC) and Weddell seals (LW) from the Danco coast, Western Antarctic Peninsula. Bayesian's Layman's isotope metrics $\delta^{15}\text{N}$ range (NR) and $\delta^{13}\text{C}$ range (CR) with their respective 95% credibility intervals are also presented. All metrics are in (‰^2).

Species	CH	SEAc	SEA_B (95% CI)	CR (95%CI)	NR (95%CI)
HL	17.23	2.82	2.81 (2.51–3.13)	2.64 (1.95–4.19)	5.34 (4.55–6.32)
HL_{high}	12.49	2.15	2.14 (1.87–2.44)	-	-
HL_{low}	9.36	1.70	1.66 (1.38–2.02)	-	-
LC	13.98	2.99	2.97 (2.49–3.49)	2.39 (1.79–3.17)	2.53 (1.79–3.41)
LW	13.74	2.13	2.14 (1.87–2.42)	2.26 (1.57–3.01)	2.06 (1.60–2.63)

Table 5

Overlap measures of isotopic niche areas (SEAc and convex hulls, the latter in parentheses) between leopard seals (population level, HL, and the two groups, low-trophic level, HL_{low} and high-trophic level, HL_{high}), crabeater seals (LC) and Weddell seals (LW) from the Danco coast, Western Antarctic Peninsula.

Species 1	Species 2	Overlap area (‰^2)	% of Sp 1 area	% of Sp 2 area
HL	LC	0.54 (8.34)	19 (48)	18 (60)
HL	LW	0.00 (2.93)	0 (17)	0 (21)
LC	LW	0.00 (0.00)	0 (0)	0 (0)
HL_{low}	HL_{high}	0.00 (6.20)	0 (66)	0 (50)
HL_{low}	LC	1.63 (7.88)	96 (84)	55 (56)
HL_{low}	LW	0.00 (0.03)	0 (0)	0 (0)
HL_{high}	LC	0.00 (5.34)	0 (43)	0 (38)
HL_{high}	LW	0.00 (2.98)	0 (23)	0 (21)

outermost contour, respectively (Fig. S7). Therefore, the subsequent mixing models were run with the set of TDF values obtained from Beltran et al. (2016) values.

Diet compositions estimated using Bayesian stable isotope mixing models revealed intra- and interspecific differences among seals (Table 6). For both HL and the two HL groups the highest dietary contributor was krill. However, fish and cephalopods also significantly contributed to the diet of the species as a whole and for the HL_{high} seals. The crabeater seals almost exclusively consumed krill, with a low contribution of fish. Weddell seals, on the other hand, showed a high proportion of fish and a lower contribution of cephalopods and penguins, while the contribution of krill seemed to be minimal (Fig. 4).

Mixing models run separately for each HL seal (Fig. 5) showed a large variation in the proportional contribution of krill compared to the other sources (cephalopods, fish, penguins and seals). The mean contribution of krill ranged from 12% (5–19%, seal HL22) to 90% (79.4–96.1%, seal HL17) (Table S2).

4. Discussion

Results presented here showed a complete niche partition between crabeater and Weddell seals inhabiting the Western Antarctic

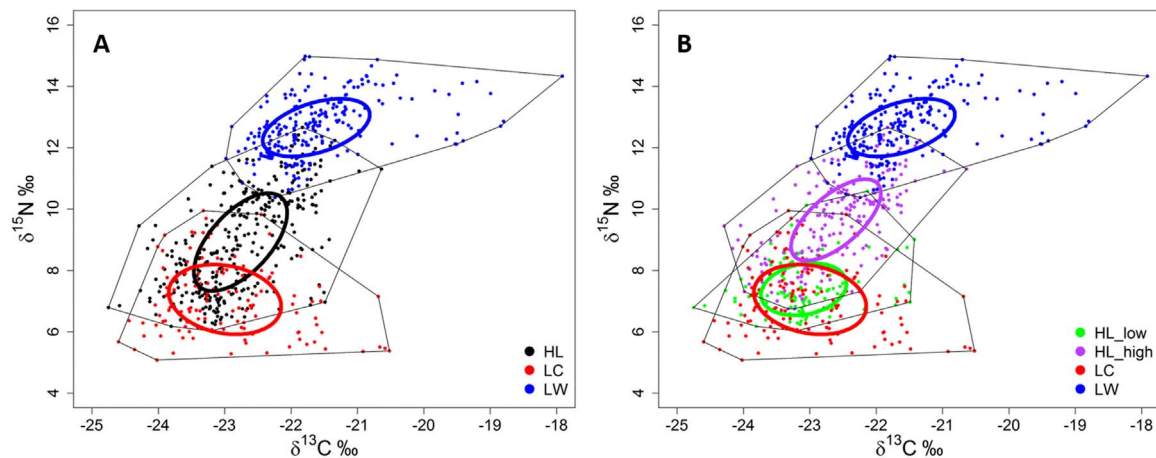


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic niches of leopard seals (population level – HL in panel A, and low- and high-trophic level groups, HL_{low} and HL_{high}, respectively in panel B), crabeater seals (LC) and Weddell seals (LW) from the Danco coast, Western Antarctic Peninsula. The colored lines enclose the standard ellipse area (SEAc) for each group estimated by SIBER analysis (Stable Isotope Bayesian Ellipses in R, Jackson et al., 2011).

Table 6

Stable isotope mixing model (simmr) results with predicted diet proportions (2.5% and 97.5% quantiles) of each prey group to the diet of leopard seals (population level, HL, and the two groups, low-trophic level, HL_{low} and high-trophic level, HL_{high}), crabeater seals (LC) and Weddell seals (LW) from the Danco coast, Western Antarctic Peninsula. Mean values are in parentheses. Values in bold are the highest prey item contribution.

Species	krill	fish	cephalopod	penguin	seal
HL	0.55–0.68 (0.62)	0.02–0.30 (0.13)	0.02–0.26 (0.11)	0.01–0.18 (0.07)	0.01–0.18 (0.07)
HL _{low}	0.79–0.90 (0.85)	0.01–0.10 (0.04)	0.01–0.10 (0.04)	0.01–0.09 (0.04)	0.01–0.09 (0.03)
HL _{high}	0.44–0.56 (0.50)	0.03–0.40 (0.20)	0.03–0.40 (0.20)	0.01–0.20 (0.08)	0.01–0.23 (0.09)
LC	0.80–0.97 (0.90)	0.03–0.20 (0.10)	–	–	–
LW	0.01–0.10 (0.04)	0.24–0.92 (0.68)	0.01–0.51 (0.14)	0.02–0.38 (0.13)	–

Peninsula, while leopard seals seemed to prey upon a broad spectrum of prey in the region, mainly showing overlapping niches with the crabeater seal. Furthermore, intraspecific niche partitioning within leopard seals was suggested, with some individuals exploring low-trophic level (i.e. krill) and others feeding also upon higher-trophic level prey, at least over the timescale analyzed here (i.e. months to up to one year).

Most of the available information on the diet of these predators is based on the short-term instantaneous analysis of prey remains in scats or stomach content analysis (e.g., Dearborn, 1965; Green and Williams, 1986; Casaux et al., 2011). These traditional methods offer a great taxonomic resolution and thus provide valuable information about the diet of these predators; however, they present some known caveats. Whenever hard parts of prey are not consumed or are completely digested, for example, they cannot be detected either in stomach or scat content analysis (Tollit et al., 1997; Bowen and Iverson, 2013). Furthermore, in the case of scat analysis, it is often difficult to assign the sample to a single individual, thus precluding the evaluation of the effect of age or sex in the diet composition of the species. The stable isotope analysis of a progressively-growing, keratinous tissue that is metabolically inert, such as whisker, provides sequential information on the diet assimilated over the timescale of growth. For the phocid leopard seals the whiskers molt annually, thus vibrissae represent growth over a few months, but no more than one year (Rogers et al., 2016). Although there is no available information on the whisker growth for crabeater and Weddell seals, it is reasonable to suppose that they follow similar growth trajectories and integrate similar feeding intervals as leopard and other seal's whiskers (Beltran et al., 2015; McHuron et al., 2016). In this context, the analysis of whisker

subsamples of these seals provided useful information on long-term diet and trophic overlap among these pack-ice seal species, otherwise difficult to study due to the difficult access to samples for stomach/feces contents, especially during winter months.

4.1. Isotopic niche partitioning among seal species around the WAP

No overlap in isotopic niches was detected between Weddell and crabeater seals, which is consistent with their, respectively, ichthyophagous (Burns et al., 1998; Casaux et al., 2011; Goetz et al., 2016) and planktophagous (Zhao et al., 2004; Hückstädt et al., 2012) feeding habits. The high nitrogen isotopic values of Weddell seals indicated their top trophic position among seals. In fact, the mixing models showed that fish and cephalopods accounted for more than 80% of WAP Weddell seals diet, while krill and benthic invertebrates were less important (Fig. 4). Cephalopods and fish are also the main components of the Weddell seals diet from the Ross Sea (Burns et al., 1998; Goetz et al., 2016) and from the northern Antarctic Peninsula (Daneri et al., 2012; Negri et al., 2016). Some animals, however, showed $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values that exceeded TDF-corrected prey isotopic values (Fig. 3) laying outside the 5% probability contour in the mixing polygons (Fig. S7). These results probably indicate that other prey items, enriched in the heavier isotopes, were consumed by these individuals. The Antarctic toothfish (*Dissostichus mawsoni*) is considered a common prey to the Weddell seals in the Ross sea, as indicated by behavioral observations and stable isotope mixing models (Goetz et al., 2016). This fish is a high trophic level predator and, therefore, show higher isotopic values than other fish species in that ecosystem (Goetz et al., 2016). Otoliths of this fish are not found in fecal or stomach content analysis as Weddell seals eat only its flesh (Ponganis and Stockard, 2007). Therefore, although this fish was not found in previous studies on diet of the LW in the WAP, it might have been consumed, leading to the high nitrogen isotope values observed in Weddell seals. Unfortunately, no isotopic values are available for *D. mawsoni* from the WAP, thus it could not be included in the *simmr* models. Moreover, Weddell seals had larger $\delta^{13}\text{C}$ range value than leopard and crabeater seals, which is likely associated with a wider range of foraging habitats. The species is probably exploring both benthic and pelagic prey in the WAP, as its excellent diving ability (Thomas and Terhune, 2009) allows it to use the entire water column to forage in the shallow shelf waters (Plotz et al., 2001; Hindell et al., 2002; Casaux et al., 2009; Costa et al., 2010; Heerah et al., 2013; Raymond et al., 2015). Therefore, the large range of $\delta^{13}\text{C}$ values found along the whiskers of Weddell seals from the Danco coast might be associated with the consumption of ^{13}C -enriched benthic and ^{13}C -depleted pelagic prey (France, 1995; Cherel and Hobson, 2007), as

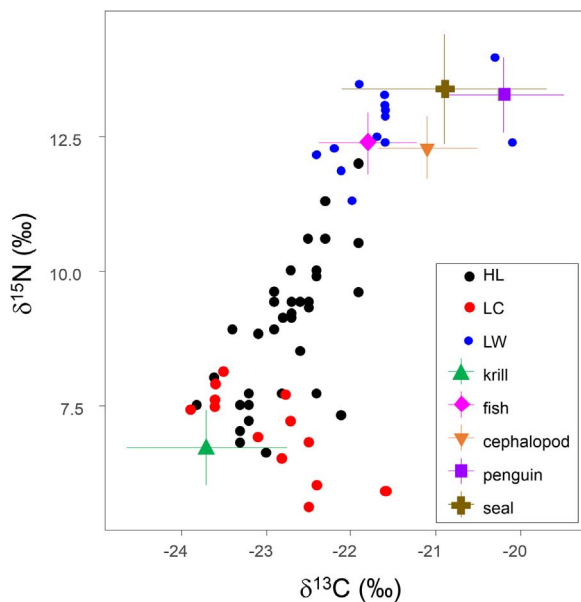


Fig. 3. Individual mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for whisker subsamples of leopard seals (*Hydrurga leptonyx*), crabeater seals (*Lobodon carcinophaga*) and Weddell seals (*Leptonychotes weddellii*) from the Danco coast, Western Antarctic Peninsula. Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, corrected for trophic discrimination factors, of their main prey obtained from literature (see Table 1 for references) are shown.

reported by Casaux et al. (2011) based on the analysis of scat samples.

Crabeater seals depend almost exclusively on Antarctic krill (Laws, 1977; Bengtson, 2009; Hückstädt et al., 2012). In the present work, Bayesian mixing models estimated a mean proportion of 90% for krill, while the other prey categories had a negligible mean contribution to their diet (Fig. 4). This result is also in agreement with the relative abundance of dietary fatty acids that are common in krill, in the blubber of crabeater seals from the Danco coast (Guerrero and Rogers,

2017). Hückstädt et al. (2012) analyzing whisker subsamples of crabeaters from Marguerite Bay area, in the southwestern Antarctic Peninsula, also found that krill represented the dominant contribution, of up to 98.3%, to the diet of this seal species. Furthermore, body mass was negatively correlated with $\delta^{15}\text{N}$ values therefore, and this was probably attributed to the mixed age sample for this species, where all animals considered as yearlings (Laws et al., 2003) showed higher mean $\delta^{15}\text{N}$ values, compared to adults. The latter also showed low temporal variability while yearlings had a peak in $\delta^{15}\text{N}$ values (LC3, LC5, LC7, LC8, LC12 and LC13, Fig. S4), towards the end of the whisker (the most recently deposited). This peak probably represents a shift towards a more ^{15}N -enriched prey. Crabeaters in the WAP showed deeper dives in winter than in summer, which was interpreted as an adaptation to follow the seasonal preferred habitat of their main prey (Burns et al., 2004, 2008). Indeed, *E. superba* is found in deeper waters during winter in the WAP (Lawson et al., 2008). Yearlings, and juveniles in general, might have lower foraging success in the greater depths where krill is found during winter, due to their reduced oxygen stores and lower lipid reserves (Burns et al., 2005; McDonald et al., 2008). Therefore, they might be forced to switch their diet to a more easy-to-capture prey. This is somewhat supported by the almost invariable $\delta^{13}\text{C}$ profiles of these yearlings in comparison to the more variable profiles of adult crabeaters (Fig. S3) which might reflect these seasonal differences in the feeding habitat along the water column (shallow vs. deep) of the latter.

Leopard seals are usually considered apex predators of the Antarctic ecosystem (Rogers, 2009). Marine mammals typically have large predator–prey ratios compared with land mammals, i.e., where large mammals feed on small prey (Tucker and Rogers, 2014a, 2014b). Yet the leopard seal can take large prey, like crabeater and Antarctic fur seal (*Arctocephalus gazella*) pups, which become important in the leopard seals diet in the austral summer when weaned pups are available (Siniff and Bengtson, 1977; Hall-Aspland and Rogers, 2007; Rogers, 2009). Information derived from scat and stomach content analysis show that leopard seals feed on a broad spectrum of prey including seals, penguins, krill and fish (Hall-Aspland and Rogers, 2004; Casaux

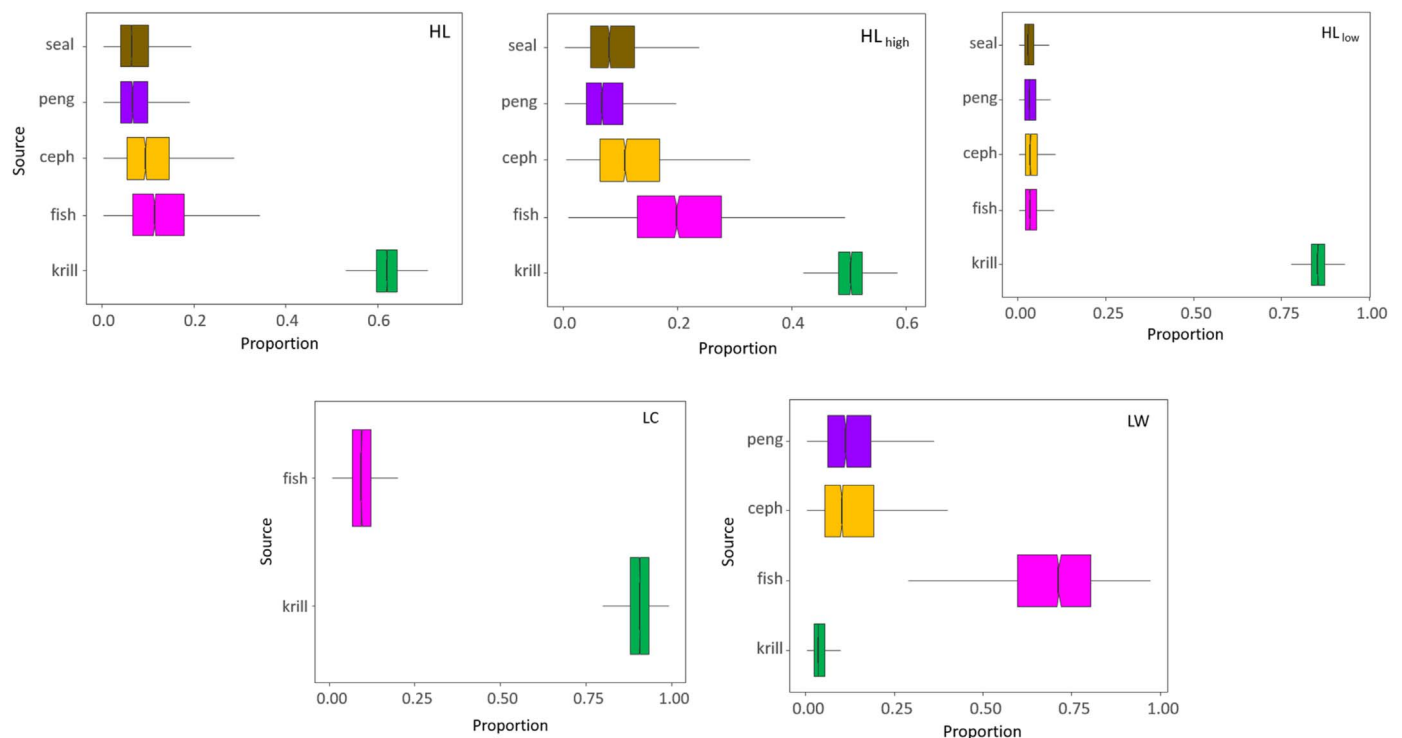


Fig. 4. Results of simmr Bayesian mixing models showing proportional estimates (mean, 25% and 75% percentiles) of diet composition for leopard seals (population level – HL, and low- and high-trophic level groups, HL_{low} and HL_{high}, respectively), crabeater seals (LC) and Weddell seals (LW) from the Danco coast, Western Antarctic Peninsula.

et al., 2011). Hall-Aspland et al. (2005a, 2005b) analyzing isotopic information in chronologically ordered whisker segments of leopard seals, reported a seasonal alternation of a vertebrate (e.g., seals, penguins) and an invertebrate (i.e., krill) diet. The high NR value found in this work (i.e., wide range of $\delta^{15}\text{N}$ values in leopard seals), together with the large support of the two trophic HL clusters found, also reveal a wide trophic diversity for leopard seals in the WAP (Layman et al., 2007). Furthermore, the wide NR range found was not related to the age as all HL individuals were classified as adults, or to the sex or body mass (Fig. 1) of the seals and these factors were not significantly correlated with the isotopic values found. Rogers et al. (2016) using a set of growth models to assign whisker segments to specific time period, showed that the krill-based diet should take place in the austral winter, while the vertebrate prey consumption occurs mainly during the austral spring/summer. In the present work the timing of the isotopic values along the whisker could not be determined, however, the individual profiles of $\delta^{15}\text{N}$ values (Fig. S2) showed switches between ^{15}N -enriched (i.e., high trophic level prey) and depleted (i.e., krill) values along the whisker length that could be compatible with the seasonal alternations of diet described (Hall-Aspland et al., 2005a; Rogers et al., 2016). On the other hand, some individuals (e.g., low trophic level, HL2 and HL24; high trophic level, HL14 and HL31, Fig. S2) seemed to maintain their preference for low/high trophic level prey throughout the year. Indeed, individual level mixing model results (Table S2, Fig. 5) showed large variation in the proportion of krill vs nektonic prey (i.e. cephalopods, fish, penguins and seals). These individual-based results coupled to the two potential groups of leopard seals in the WAP may reflect some degree of individual foraging specialization in this species – although, as we do not know the whiskers growth pattern, it may also reflect diet choices over a shorter period. In order to test this hypothesis, it is necessary to confirm if the time frame integrated by leopard seal vibrissae is representative of the entire trophic niche of the individual (Araújo et al., 2011; Rogers et al., 2016). Nevertheless, results found in this work show the high trophic plasticity of the species, which can be crucial to overcome future scenarios of ecosystem change in the WAP.

The low-trophic level group of leopard seals (HL_{low}) showed a high overlapped isotopic niche with crabeater seals. Indeed, mixing models also estimated a mean relative contribution of 86% of krill for this group. Krill was also important in the diet of the high-trophic level group of leopard seals (mean contribution of 52%), but fish and cephalopods also significantly contributed to the diet (Fig. 4). Although the HL_{high} isotopic niche was completely segregated in the δ -space,

some whisker samples showed isotopic values that overlapped both to those of the Weddell and the crabeater seals (and HL_{low} group), representing a wide trophic plasticity of the species (Siniff and Bengtson, 1977; Hall-Aspland and Rogers, 2004, 2007; Rogers, 2009; Hall-Aspland et al., 2005a, 2005b, 2011; Casaux et al., 2011; Guerrero et al., 2016). Although leopard seals are widely distributed on the pack ice (Southwell et al., 2008; Rogers et al., 2013), individual seals have a restricted home range (Rogers et al., 2005; Meade et al., 2015), which is reflected in the small range of $\delta^{13}\text{C}$ values observed along the whiskers of the individuals from the Danco Coast.

Although sampling years were not consistent among seals, all three species were sampled in the austral summer of 2014. Furthermore, year was not a significant variable affecting isotopic values of the three species thus the isotopic niche partition and overlap detected in the present study is probably representative of the true trophic relationship among these seals in the WAP. Goetz et al. (2016) reported interannual variation in the isotopic values of high turnover tissues (i.e. blood) of Weddell seals from the Ross sea. However, isotopic values in whiskers from the same individuals did not vary among years, the difference being attributed to the long-term time integration of the whisker and the single-point, time restricted information gathered from the isotopic analysis of red blood cells. Therefore, the analysis of serially sampled whiskers must have smoothed potential interannual variation in the isoscapes of the WAP (Seyboth et al., in this issue).

Another caveat of the study design is the use of published isotopic values from prey that were not sampled in the same years of the seals. Interannual variations at the base of the trophic web and/or the trophic ecology of the prey can potentially affect their isotopic values (Seyboth et al., in this issue) and thus introduce undesired biases in the mixing models. However, due to the striking differences in the mixing models results among the three seals and the dietary broad-scale approach used (i.e. not focused on a taxonomically refined prey database) large effects on the results were not expected. Nevertheless, future taxonomically refined mixing models based on a contemporary prey/predator isotopic data base is likely to provide a more refined insight into the feeding habits of these seals in the WAP. Furthermore, species-specific whisker growth models for Weddell and crabeater seals, coupled to a follicle specific sampling procedure for whiskers will add important information about the seasonal changes in feeding habits among and within the assemblage of seals that inhabits the WAP.

5. Conclusions

This study is the first to compare isotopic niches of three Antarctic seals from the Western Antarctic Peninsula. Our results indicate species-specific differences in trophic ecology and intraspecific variation in the case of leopard seals. Crabeater and leopard seals seem to have a strong and a considerable dependence on krill, respectively. Although the WAP is characterized by an unusual high production of Antarctic krill (Atkinson et al., 2004; Forcada et al., 2012), the large community of vertebrate predators that feed upon this resource (e.g. crabeater seals, Adélie penguins, Antarctic fur seals, and baleen whales) should be especially vulnerable under future scenarios of reduction of krill biomass (Atkinson et al., 2008; Seyboth et al., 2016). Antarctic krill is a key species in the Southern Ocean, acting as a trophic link between primary production and these secondary consumers (Ducklow et al., 2007). Current trends in sea-ice extent decline in the WAP will allow an expansion of the krill fisheries to more coastal habitats during winter, where large crowds of over-wintering krill are found (Reiss et al., 2017). This overlap will increase the negative interaction between these fisheries and krill consumers, thus considerably affecting the future maintenance of their populations in the WAP. On the other hand, undergoing changes in the sea ice cover of the WAP due to climate change (Ducklow et al., 2007) would also affect these predators by limiting the available breeding and foraging habitat, especially for crabeater and Weddell seals (Costa et al., 2010; Forcada et al., 2012). Under the

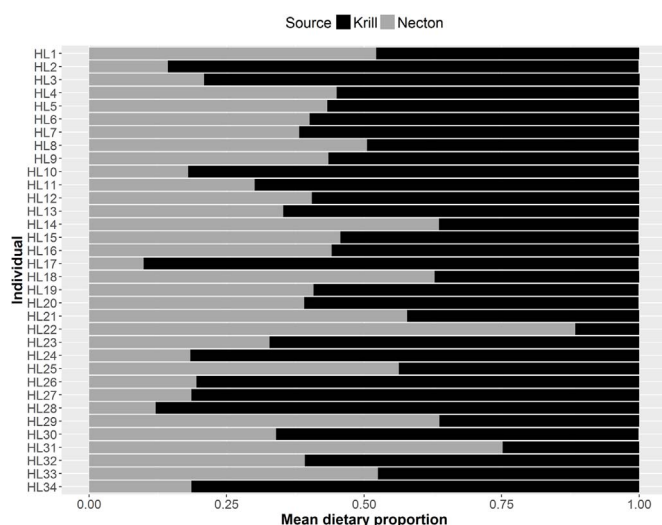


Fig. 5. Individual variation in the contribution of krill and nekton prey (cephalopods, fish, penguins and seals) to the diet of leopard seals from the Danco coast, Western Antarctic Peninsula.

current drastic environmental changes in the WAP, continuing to monitor WAP seal diets and the relative contribution of krill to them will help understand the degree to which climate change may alter the population dynamics of these upper trophic level species. In this context, regardless of the known caveats of the method and the variable temporal window that whisker may represent (i.e. months to years), obtaining long-term dietary records of these predators provides a powerful tool to study changes in the habitat use and diet that could be related to ecosystem alterations (Huang et al., 2011). Indeed, obtaining equivalent data from traditional sampling methods (i.e. stomach or fecal contents) is usually constrained to the austral summer periods due to the logistical challenges of accessing these animals in the winter months. Therefore, the low cost, minimal invasive whisker sampling is encouraged in order to record long-term changes in these predators' trophic niches.

Acknowledgements

We would like to thank the team of Base Primavera for their support during field work and Ana Bárbara Broni who collaborated with the sample processing. The immobilisation and sampling of leopard, crabeater and Weddell seals within the Antarctic Specially Protected Area No. 134 were approved by the Dirección Nacional del Antártico, Program of Environmental Management and Tourism (PGAyT), Buenos Aires, Argentina (Permit no. 8). Research procedures were also reviewed and approved by the University of New South Wales' Animal Care and Ethics Committee protocol numbers 08/103B and 11/112A to TR. Field work was supported and funded by the Dirección Nacional del Antártico, Instituto Antártico Argentino PICTA 01–2010 and by the Australian Research Council Linkage Program, number LP0989933. National Council for Research and Technological Development (CNPq) provided a research fellowship to ERS (PQ 307846/2014-8). SB is currently postdoctoral fellow of the Coordination for the Improvement of Higher Education Personnel (CAPES-PNPD). This work is a contribution of the research groups *Ecologia e Conservação da Megafauna Marinha-EcoMega/CNPq*, Grupo de Oceanografía de Altas Latitudes – GOAL/CNPq and the INTERBIOTA Project (CNPq Grant number 407889/2013-2).

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2017.11.005>.

References

- Acevedo, J., Carreño, J., Torres, D., Aguayo-Lobo, A., Letelier, S., 2015. Cephalopod remains in scats of Weddell seals (*Leptonychotes weddellii*) at Cape Sheriff, South Shetland Islands, Antarctica. *Polar Biol.* 38, 1559–1564.
- Araújo, M.S., Bolnick, D.I., Layman, C.A., 2011. The ecological causes of individual specialisation. *Ecol. Lett.* 14, 948–958.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Progr. Ser.* 362, 1–23.
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., MacLeod, H., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J. Anim. Ecol.* 73, 1007–1012.
- Beltran, R.S., Sadou, M.C., Condit, R., Peterson, S.H., Reichmuth, C., Costa, D.P., 2015. Fine-scale whisker growth measurements can reveal temporal foraging patterns from stable isotope signatures. *Mar. Ecol. Progr. Ser.* 523, 243–253.
- Beltran, R.S., Peterson, S.H., McHuron, E.A., Reichmuth, C., Hückstädt, L.A., Costa, D.P., 2016. Seals and sea lions are what they eat, plus what? Determination of trophic discrimination factors for seven pinniped species. *Rapid Commun. Mass Spectrom.* 30, 1115–1122.
- Bengtson, J.L., 2009. Crabeater seal *Lobodon carcinophaga*. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), *Encyclopedia of Marine Mammals*. Academic Press, San Diego, California, USA, pp. 290–292.
- Bombosch, A., Solov'yev, B., 2017. Weddell seal (*Leptonychotes weddellii*) killing Gentoo penguin (*Pygoscelis papua*) at Neko Harbour, Antarctic Peninsula. *Polar Biol.* 40, 1899–1902.
- Bowen, W.D., Iverson, S.J., 2013. Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. *Mar. Mamm. Sci.* 29, 719–754.
- Burns, J.M., Trumble, S.J., Castellini, M.A., Testa, J.W., 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biol.* 19, 272–282.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J., Gales, N.J., McDonald, B., Trumble, S.J., Crocker, D.E., 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. *Deep Sea Res. Part II: Trop. Stud. Oceanogr.* 51, 2279–2303.
- Burns, J.M., Costa, D.P., Frost, K., Harvey, J.T., 2005. Development of body oxygen stores in harbor seals: effects of age, mass, and body composition. *Physiol. Biochem. Zool.* 78, 1057–1068.
- Burns, J.M., Hindell, M.A., Bradshaw, C.J.A., Costa, D.P., 2008. Fine-scale habitat selection of crabeater seals as determined by diving behavior. *Deep Sea Res. Part II: Trop. Stud. Oceanogr.* 55, 500–514.
- Casaux, R., Baroni, A., Ramón, A., 2006. The diet of the Weddell Seal *Leptonychotes weddellii* at the Danco Coast, Antarctic Peninsula. *Polar Biol.* 29, 257–262.
- Casaux, R., Baroni, A., Ramón, A., Carlini, A., Bertolin, M., DiPrinzio, C., 2009. Diet of the leopard seal *Hydrurga leptonyx* at the Danco Coast, Antarctic Peninsula. *Polar Biol.* 32, 307–310.
- Casaux, R., Bertolin, M.L., Carlini, A., 2011. Feeding habits of three seal species at the Danco Coast, Antarctica: a re-assessment. *Polar Biol.* 34, 1615–1620.
- Cherel, Y., Hobson, K.A., 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Progr. Ser.* 329, 281–287. <http://dx.doi.org/10.3354/meps329281>.
- Costa, D.P., Hückstädt, L.A., Crocker, D.E., McDonald, B.L., Goebel, M.E., Fedak, M.A., 2010. Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integr. Comp. Biol.* 50, 1018–1030.
- Dalerum, F., Angerbjörn, A., 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia* 144, 647–658.
- Daneri, G.A., Carlini, A.R., Negri, A., Allcock, A.L., Corbalán, A., 2012. Predation on cephalopods by Weddell seals, *Leptonychotes weddellii*, at Hope Bay, Antarctic Peninsula. *Polar Biol.* 35, 585–592.
- Dearborn, J.H., 1965. Food of Weddell seals at McMurdo sound, Antarctica. *J. Mammal.* 46, 37–43.
- Deniro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42, 495–506.
- Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., Fraser, W., 2007. Marine pelagic ecosystems: the west Antarctic Peninsula. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 362, 67–94.
- Ducklow, H.W., Fraser, W.R., Meredith, M.P., Stammerjohn, S.E., Doney, S.C., Martinson, D.G., Sailley, S.F., Schofield, O.M., Steinberg, D.K., Venables, H.J., Amsler, C.D., 2013. West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. *Oceanography* 26, 190–203. <http://dx.doi.org/10.5670/oceanog.2013.62>.
- Dunton, K.H., 2001. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements of antarctic peninsula fauna: trophic relationships and assimilation of benthic seaweeds 1. *Am. Zool.* 41, 99–112.
- Forcada, J., Trathan, P.N., Boveng, P.L., Boyd, I.L., Burns, J.M., Costa, D.P., Fedak, M., Rogers, T.L., Southwell, C.J., 2012. Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biol. Conserv.* 149, 40–50.
- France, R.L., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Progr. Ser.* 124, 307–312.
- Goetz, K.T., Burns, J.M., Hückstädt, L.A., Shero, M.R., Costa, D.P., 2016. Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. *Deep Sea Res. Part II* 140, 36–44. <http://dx.doi.org/10.1016/j.dsr2.2016.05.017>.
- Green, K., Williams, R., 1986. Observations on food remains in faeces of elephant, leopard and crabeater seals. *Polar Biol.* 6, 43–45.
- Guerrero, A.I., Negrete, J., Márquez, M.E.I., Mennucci, J., Zaman, K., Rogers, T.L., 2016. Vertical fatty acid composition in the blubber of leopard seals and the implications for dietary analysis. *J. Exp. Mar. Biol. Ecol.* 478, 54–61.
- Guerrero, A.I., Rogers, T.L., 2017. Blubber fatty acid composition and stratification in the crabeater seal, *Lobodon carcinophaga*. *J. Exp. Mar. Biol. Ecol.* 491, 51–57.
- Hall-Aspland, S.A., Rogers, T.L., 2004. Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol.* 27, 729–734.
- Hall-Aspland, S.A., Rogers, T.L., Canfield, R.B., 2005a. Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. *Mar. Ecol. Progr. Ser.* 305, 249–259.
- Hall-Aspland, S.A., Hall, A.P., Rogers, T.L., 2005b. A new approach to the solution of the linear mixing model for a single isotope: application to the case of an opportunistic predator. *Oecologia* 143, 143–147.
- Hall-Aspland, S., Rogers, T., 2007. Identification of hairs found in leopard seal (*Hydrurga leptonyx*) scats. *Polar Biol.* 30, 581.
- Hall-Aspland, S., Rogers, T., Canfield, R., Tripovich, J., 2011. Food transit times in captive leopard seals (*Hydrurga leptonyx*). *Polar Biol.* 34, 95–99.
- Heerah, K., Andrews-Goff, V., Williams, G., Sultan, E., Hindell, M., Patterson, T., Charrassin, J.B., 2013. Ecology of Weddell Seals during winter: influence of environmental parameters on their foraging behavior. *Deep Sea Res. Part II: Trop. Stud. Oceanogr.* 88, 23–33.
- Higgins, D.P., Rogers, T.L., Irvine, A.D., Hall-Aspland, S., 2002. The use of midazolam/pethidine and tiletamine/zolazepam combinations for the chemical restraint of leopard seals (*Hydrurga leptonyx*). *Mar. Mamm. Sci.* 18, 483–499.
- Hindell, M.A., Harcourt, R.G., Waas, J.R., Thompson, D., 2002. Fine-scale, three dimensional spatial use of diving by lactating female Weddell seals *Leptonychotes weddellii*. *Mar. Ecol. Progr. Ser.* 242, 275–284.

- Hirons, A.C., Schell, D.M., St. Aubin, D.J., 2001. Growth rates of vibrissae of harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumatopias jubatus*). *Can. J. Zool.* 79, 1053–1061.
- Hobson, K.A., Schell, D.M., Renouf, D., Noseworthy, E., 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can. J. Fish. Aquat. Sci.* 53, 528–533.
- Huang, J., Sun, L., Wang, X., Huang, T., 2011. Ecosystem evolution of seal colony and the influencing factors in the 20th century of Fildes Peninsula, West Antarctica. *J. Environ. Sci.* 23, 1431–1436.
- Hückstädt, L.A., Burns, J.M., Koch, P.L., McDonald, B.I., Crocker, D.E., Costa, D.P., 2012. Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. *Mar. Ecol. Progr. Ser.* 455, 287–301.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses. *J. Anim. Ecol.* 80, 595–602.
- Kaufman, L., Rousseeuw, P.J., 1990. *Finding Groups in Data: An Introduction to Cluster Analysis*. Wiley, New York, New York, USA.
- Kokubun, N., Choy, E.J., Kim, J.H., Takahashi, A., 2015. Isotopic values of Antarctic Krill in relation to foraging habitat of penguins. *Ornithol. Sci.* 14, 13–20.
- Laws, R.M., 1977. Seals and whales of the Southern Ocean. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 279, 81–96.
- Laws, R.M., Baird, M.M., Bryden, M.M., 2003. Size and growth of the crabeater seal *Lobodon carcinophagus* (Mammalia: carnivora). *J. Zool.* 259, 103–108.
- Lawson, G.L., Wiebe, P.H., Ashjian, C.J., Stanton, T.K., 2008. Euphasiid distribution along the Western Antarctic Peninsula – Part B: distribution of euphasiid aggregations and biomass, and associations with environmental features. *Deep Sea Res. Part II: Trop. Stud. Oceanogr.* 55, 432–454.
- Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88, 42–48.
- Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. <http://dx.doi.org/10.1111/2041-210X.12512>.
- Lowry, L.F., Testa, J.W., Calvert, W., 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biol.* 8, 475–478.
- Lynch, H.J., Naveen, R., Trathan, P.N., Fagan, W.F., 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93, 1367–1377.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2017. *cluster: Cluster Analysis Basics and Extensions*. R package version 2.0.6. <https://cran.r-project.org/web/packages/cluster/index.html>.
- Martínez del Río, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biol. Rev.* 84, 91–111. <http://dx.doi.org/10.1111/j.1469-185X.2008.00064.x> PMID: 19046398.
- McDonald, B.I., Crocker, D.E., Burns, J.M., Costa, D.P., 2008. Body condition as an index of winter foraging success in crabeater seals (*Lobodon carcinophaga*). *Deep Sea Res. Part II* 55, 515–522.
- McHuron, E.A., Walcott, S.M., Zeligs, J., Skrovan, S., Costa, D.P., Reichmuth, C., 2016. Whisker growth dynamics in two North Pacific pinnipeds: implications for determining foraging ecology from stable isotope analysis. *Mar. Ecol. Progr. Ser.* 554, 213–224.
- Meade, J., Ciaglia, M.B., Slip, D.J., Negrete, J., Márquez, M.E.I., Mennucci, J., Rogers, T.L., 2015. Spatial patterns in activity of leopard seals *Hydrurga leptonyx* in relation to sea ice. *Mar. Ecol. Progr. Ser.* 521, 265–275.
- Mincks, S.L., Smith, C.R., Jeffreys, R.M., Sumida, P.Y., 2008. Trophic structure on the West Antarctic Peninsula shelf: detritivory and benthic inertia revealed by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Deep Sea Res. Part II* 55, 2502–2514.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Negri, A., Daneri, G.A., Ceia, F., Vieira, R., Cherel, Y., Coria, N.R., Corbalán, A., Xavier, J.C., 2016. The cephalopod prey of the Weddell seal, *Leptonychotes weddellii*, a biological sampler of the Antarctic marine ecosystem. *Polar Biol.* 39, 561–564.
- Newsome, S.D., Martínez del Río, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotope ecology. *Front. Ecol. Environ.* 5, 429–436.
- Newsome, S.D., Tinker, M.T., Monson, D.H., Ofedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L., Estes, J.A., 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90, 961–974.
- Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci.* 26, 509–572.
- Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5, e9672.
- Parnell, A., 2016. *simmr-package A Stable Isotope Mixing Model*. Version 0.3. <https://cran.r-project.org/web/packages/simmr/>.
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18, 293–320.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-PLUS*. Springer, New York.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACK, Heisterkamp, S., Bert Van Willigen, 2017. *Linear and Nonlinear Mixed Effects Models. Fit and compare Gaussian linear and nonlinear mixed-effects models*. Version 3.1-131. <https://cran.r-project.org/web/packages/nlme/index.html>.
- Plotz, J., Bornemann, H., Kmst, R., Schroder, A., Bester, M., 2001. Foraging behaviour of Weddell seals, and its ecological implications. *Polar Biol.* 24, 901–909.
- Polito, M.J., Goebel, M.E., 2010. Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. *J. Exp. Mar. Biol. Ecol.* 395, 1–9.
- Polito, M.J., Lynch, H.J., Naveen, R., Emslie, S.D., 2011. Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding *Pygoscelis* spp. penguins. *Mar. Ecol. Progr. Ser.* 421, 265–277.
- Polito, M.J., Reiss, C.S., Trivelpiece, W.Z., Patterson, W.P., Emslie, S.D., 2013. Stable isotopes identify an ontogenetic niche expansion in Antarctic krill (*Euphausia superba*) from the South Shetland Islands, Antarctica. *Mar. Biol.* 160, 1311–1323.
- Ponganis, P.J., Stockard, T.K., 2007. Short note: the Antarctic toothfish: how common a prey for Weddell seals? *Antarct. Sci.* 19, 441–442.
- R Development Core Team, 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Vienna, Austria. ISBN 3-900051-07-0. Available: <http://www.r-project.org/>.
- Raymond, B., Lea, M.A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.B., Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* 38, 121–129.
- Reiss, C.S., Cossio, A., Santora, J.A., Dietrich, K.S., Murray, A., Mitchell, B.G., Walsh, J., Weiss, E.L., Gimpel, C., Jones, C.D., Watters, G.M., 2017. *Mar. Ecol. Progr. Ser.* 568, 1–16.
- Rogers, T.L., Hogg, C.J., Irvine, A., 2005. Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol.* 28, 456–463.
- Rogers, T.L., 2009. The leopard seal, *Hydrurga leptonyx*. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), *Encyclopedia of Marine Mammals*, Second edition. Academic Press, San Diego, California, USA, pp. 673–674.
- Rogers, T.L., Ciaglia, M.B., Klinck, H., Southwell, C., 2013. Density can be misleading for low-density species: benefits of passive acoustic monitoring. *PLoS One* 8, e52542.
- Rogers, T.L., Fung, J., Slip, D., Steindler, L., O'Connell, T.C., 2016. Calibrating the time span of longitudinal biomarkers in vertebrate tissues when fine-scale growth records are unavailable. *Ecosphere* 7. <http://dx.doi.org/10.1002/ecs2.1449>.
- Schell, D.M., Saupe, S.M., Haubenstein, N., 1989. Bowhead Whale (*Balaena mysticetus*) growth and feeding as estimated by ^{13}C techniques. *Mar. Biol.* 103, 433–443.
- Seyboth, E., Groch, K.R., Dalla Rosa, L., Reid, K., Flores, P.A.C., Secchi, E.R., 2016. Southern right whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Sci. Rep.* 6, 28205.
- Seyboth, E., Botta, S., Mendes, C.R.B., Negrete, J., Dalla Rosa, L., Secchi, E.R., 2017. Isotopic evidence of the effect of warming on the Northern Antarctic Peninsula ecosystem. *Deep Sea Res. II* (In this issue).
- Siniff, D.B., Bengtson, J.L., 1977. Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. *J. Mamm.* 58, 414–416.
- Smith, J.A., Mazumder, D., Suthers, I.M., Taylor, M.D., 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Methods Ecol. Evol.* 4, 612–618.
- Southwell, C., Paxton, C.G., Borchers, D., Boveng, P., Rogers, T., William, K., 2008. Uncommon or cryptic? Challenges in estimating leopard seal abundance by conventional but state-of-the-art methods. *Deep Sea Res. Part I* 55, 519–531.
- Southwell, C., Bengtson, J., Bester, M.N., Schytte-Blix, A., Bornemann, H., Boveng, P., Cameron, M., Forcada, J., Laake, J., Nordøy, E., Plötz, J., 2012. A review of data on abundance, trends in abundance, habitat utilisation and diet for Southern Ocean ice-breeding seals. *CCAMLR Sci.* 19, 49–74.
- Thomas, J.A., Terhune, J., 2009. Weddell seal, *Leptonychotes weddellii*. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), *Encyclopedia of Marine Mammals*, Second edition. Academic Press, San Diego, California, USA, pp. 1217–1219.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., Slade, N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57, 32–37.
- Tollit, D.J., Steward, M.J., Thompson, P.M., Pierce, G.J., Santos, M.B., Hughes, S., 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Can. J. Fish. Aquat. Sci.* 54, 105–118.
- Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc. Natl. Acad. Sci. USA* 108, 7625–7628.
- Tucker, M.A., Rogers, T.L., 2014a. Examining the prey mass of terrestrial and aquatic carnivorous mammals: minimum, maximum and range. *PLoS One* 9, e106402.
- Tucker, M.A., Rogers, T.L., 2014b. Examining predator–prey body size, trophic level and body mass across marine and terrestrial mammals. *Proc. R. Soc. Lond. B: Biol. Sci.* 281, 2014–2103.
- van den Hoff, J., Fraccaro, R., Mitchell, P., Field, I., McMahon, C., Burton, H., Blanchard, W., Duignan, P., Rogers, T., 2005. Estimating body mass and condition of leopard seals by allometrics. *J. Wildl. Manag.* 69, 1015–1023.
- Witteveen, B.H., Wynne, K.M., 2016. Trophic niche partitioning and diet composition of sympatric fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) in the Gulf of Alaska revealed through stable isotope analysis. *Mar. Mamm. Sci.* 32, 1319–1339.
- Zhao, L., Castellini, M., Mau, T., Trumble, S., 2004. Trophic interactions of Antarctic seals as determined by stable isotope signatures. *Polar Biol.* 27, 368–373.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York.